Non-Consumptive Effects of Spiders and Ants:

Does Fear Matter in Terrestrial Interaction Webs?

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Accepted Dissertation thesis for the partial fulfilment of the requirements for a
Doctor of Natural Sciences
Fachbereich 7: Natur- und Umweltwissenschaften
Universität Koblenz-Landau

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Date of the oral examination:
2 July 2014

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Abstract

Most animals suffer from predators. Besides killing prey, predators can affect prey physiology, morphology and behaviour. Spiders are among the most diverse and frequent predators in terrestrial ecosystems. Our behavioural arena experiments revealed that behavioural changes under spider predation risk are relatively scarce among arthropods. Wood crickets (*Nemobius sylvestris*), in particular, changed their behaviour in response to cues of various spider species. Thereby, more common and relatively larger spider species induced stronger antipredator behaviour in crickets.

Behavioural changes under predation risk are expected to enhance predator avoidance, but they come at a cost. Crickets previously confronted with cues of the nursery web spider (*Pisaura mirabilis*) were indeed more successful in avoiding predation. Surprisingly, crickets slightly increased food uptake and lost less weight under predation risk, indicating that crickets are able to compensate for short-term cost under predation risk. In a following plant choice experiment, crickets strongly avoided plants bearing spider cues, which in turn reduced the herbivory on the respective plants.

Similar to spiders, ants are ubiquitous predators and can have a strong impact on herbivores, but also on other predators. Juvenile spiders increased their propensity for long-distance dispersal if exposed to ant cues. Thus, spiders use this passive dispersal through the air (ballooning) to avoid ants and colonise new habitats.

In a field experiment, we compared arthropod colonisation between plants bearing cues of the nursery web spider and cue-free plants. We followed herbivory during the experimental period and sampled the arthropod community on the plants. In accordance with the plant choice experiment, herbivory was reduced on plants bearing spider cues. In addition, spider cues led to changes in the arthropod community: smaller spiders and black garden ants (*Lasius niger*) avoided plants bearing spider cues. In contrast, common red ants (*Myrmica rubra*) increased the recruitment of workers, possibly to protect their aphids.

Although behavioural changes were relatively rare on filter papers bearing spider cues, more natural experimental setups revealed strong and far-reaching effects of predation risk. We further suggest that risk effects influence the spatial distribution of herbivory, rather than reduce overall herbivory that is expected if predators kill herbivores. Consequently, the relative importance of predation and risk effects is crucial for the way predators affect lower trophic levels.

Zusammenfassung

Die meisten Tiere haben natürliche Feinde. Neben dem Töten von Beute (Prädation), können Räuber auch die Physiologie, Morphologie und das Verhalten von Beutetieren beeinflussen. Spinnen sind eine ausgesprochen diverse und häufige Räubergruppe in terrestrischen Ökosystemen. Unsere Verhaltensexperimente haben gezeigt, dass nur wenige Insekten- und Spinnenarten das Verhalten in der Anwesenheit von Spinnengeruchstoffen ändern. Besonders Waldgrillen (*Nemobius sylvestris*) änderten ihr Verhalten aufgrund von Geruchsstoffen mehreren Spinnenarten. Dabei bewirkten Geruchstoffe von relativ größeren und häufigeren Spinnenarten stärkere Verhaltensänderungen.

Verhaltensänderungen unter Prädationsrisiko erhöhen die Überlebensrate von Beutetieren, sind aber oft mit Kosten verbunden. Grillen, die vorher schon mit Geruchstoffen der Listspinne (*Pisaura mirabilis*) konfrontiert wurden, konnten den Spinnen tatsächlich erfolgreicher entkommen. Während des Experiments haben Grillen unter Prädationsrisiko geringfügig mehr gefressen und weniger Gewicht verloren als Kontrollgrillen. Dies deutet darauf hin, dass Grillen durch das Prädationsrisiko verursachte Kosten kurzzeitig kompensieren können. In einem Wahlexperiment bevorzugten Grillen Pflanzen ohne Spinnengeruchsstoffe. Infolgedessen wurde an Pflanzen mit Spinnengeruchsstoffen weniger gefressen.

Auch Ameisen sind allgegenwärtige Räuber und können einen starken Einfluss auf Pflanzenfresser (Herbivore) aber auch auf andere Räuber haben. Wenn junge Spinnen mit Ameisengeruchsstoffen konfrontiert wurden, stieg ihre Bereitschaft sich über größere Entfernungen auszubreiten. Junge Spinnen nutzen diese passive Ausbreitung über die Luft ('ballooning') um Ameisen zu entkommen und neue Lebensräume zu besiedeln.

In einem Freilandexperiment haben wir die Besiedlung von Pflanzen durch Arthropoden in Abhängigkeit von Spinnengeruchsstoffen untersucht. Dabei haben wir den Fraß an den Blättern und die Tiergemeinschaften erfasst. Vergleichbar zum Pflanzenwahlversuch im Labor wurde an Pflanzen mit Spinnengeruchsstoffen weniger gefressen. Zusätzlich konnten wir Veränderungen in den Tiergemeinschaften feststellen: Kleine Spinnen und die Schwarze Gartenameise (*Lasius niger*) haben Pflanzen mit Spinnengeruchsstoffen gemieden. Im Gegensatz dazu stieg die Anzahl der Arbeiterinnen der Roten Gartenameise (*Myrmica rubra*), möglicherweise um ihre Blattläuse gegen die drohende Gefahr zu verteidigen.

Obwohl Verhaltensänderungen auf Filterpapieren mit Spinnengeruchsstoffen selten waren, haben unsere Experimente unter natürlicheren Bedingungen deutliche und weitreichende Reaktionen auf die mögliche Anwesenheit von Spinnen (Risikoeffekte) gezeigt. Unsere Resultate legen nahe, dass Risikoeffekte von Räuber die räumliche Verteilung von Pflanzenfraß verändern. Die Gesamtherbivorie wurde allerdings nicht reduziert, was erwartet wird wenn Räuber Pflanzenfresser töten. Wie stark sich Prädation und Risikoeffekte relativ auf die Beute auswirken ist entscheidend für den Einfluss von Räuber auf niedrigere Nahrungsebenen.

Chapter 1

General introduction

Roman Bucher

"Fear is a powerful motivator, perhaps the most powerful of all motivators, and is felt by animals as well as humans."
Joel Berger (2010)

Ecology of fear

During their life time animals have to balance many demands including foraging, migration, courtship and predator avoidance. In doing so, individuals may fail to obtain a suitable food source or mating partner in a short time perspective, but they may succeed during following attempts. However, the failure to avoid predation is unforgiven. Thus, animals are expected to adaptively avoid predation risk – to fear predators (Lima and Dill 1990). Animals can perceive predation risk via visual, acoustic, vibratory and chemical cues (Caro 2005). **Chemical cues** are of particular interest, because they can persist in the environment for some time after the predator has left (Kats and Dill 1998; Ferrari *et al.* 2010). Thereby, they can inform many prey individuals simultaneously without any saturation effect that typically occurs if predators eat prey (i.e. functional response). The idea that effects of predation risk complement effects of killing prey led to the concept of non-consumptive effects. **Non-consumptive effects** are all direct effects of predators on prey that do not involve killing individuals (i.e. consumptive effects or density-mediated effects) (Abrams 1995; Abrams 2007; **Figure 1b**). Non-consumptive effects manifest themselves in prey by characteristic changes of their traits under predation risk. Thus, non-consumptive effects are considered as a special case of the more general trait-mediated effects that can be initiated by trophic levels other than predators (Abrams 2007; Schoener and Spiller 2012). Such dynamic traits commonly include physiology, morphology and behaviour of prey.

The so called 'fight-or-flight' response to predation risk can induce **physiological stress**, which influences metabolic rates and increases the release of stress proteins and of antioxidant enzymes (Rovero *et al.* 1999; Pauwels *et al.* 2005; Slos and Stoks 2008). Higher levels of these energetically costly substances reduced the growth rate of the damselfly *Enallagma cyathigerum* under predation risk of sticklebacks (Slos and Stoks 2008). **Morphological changes** under predation risk seem to be less common (Schoener and Spiller 2012). However, the Tollrian (1990) textbook example increased the awareness of non-consumptive effects among ecologists. In his experiment, genetically identical *Daphnia cucullata* developed higher helmets in the presence of chemical cues of the predatory mosquito larvae *Chaoborus flavicans*. These helmet-like structures are expected to reduce

predation rate by the mosquito larvae. So far, the vast majority of non-consumptive effect studies investigate effects of predation risk on prey behaviour (Werner and Peacor 2003; Bolnick and Preisser 2005). In contrast to morphological changes (developmental plasticity), prey individuals can change their behaviour immediately in response to acute predation risk. **Antipredator behaviour** can be divided into reduction or increase in general activity (to reduce detection *versus* to escape; Lima and Dill 1990). The choice of antipredator strategy can depend on species traits such as predator hunting mode and prey mobility (Caro 2005). To escape from predators is energy demanding (Ydenberg and Dill 1986) and hiding reduces the time spent feeding or searching for mates. Thus, animals are expected to trade-off anipredator behaviour against incurred fitness costs (Sih 1980; Houston *et al.* 1993; Lind and Cresswell 2005).

Extending the trophic ladder

In a three-level **trophic cascade**, predators release primary producers from consumers by killing herbivores (Hairston *et al.* 1960; Rosenzweig 1973; Oksanen *et al.* 1981; **Figure 1a**). This compelling argument in favour of top-down control became famous as the 'green world hypothesis' (Hairston *et al.* 1960). It highlights the pervasive role of predators in controlling ecosystems and initiated an intensive and ongoing controversy about the relative importance of top-down and bottom-up regulation of ecosystems. As outlined above, non-consumptive effects of predators act often in concert with predation. Changes in prey foraging behaviour under predation risk are especially important because they can extend the influence of non-consumptive effects into lower trophic levels. Consequently, cascades are not solely restricted to consumptive interactions: non-consumptive effects of predators on prey can indirectly affect primary producers as well. This transmission of effects via changes in traits of intermediate species has been termed **trait-mediated indirect effects** (Abrams 1995; Abrams 2007; **Figure 1c**). Trait-mediated indirect effects can reduce herbivory by reducing feeding activity or time spent feeding (Trussell *et al.* 2003). In addition, herbivores may avoid plants previously occupied by a predator. Grasshoppers switch from feeding on grasses to consumption of herbs under predation risk (Beckerman *et al.* 1997). Thus, behavioural responses of prey to predators such as changes in feeding activity and shifts towards safer habitats can have a strong impact on ecosystems (Schmitz *et al.* 2004; Thaler and Griffin 2008).
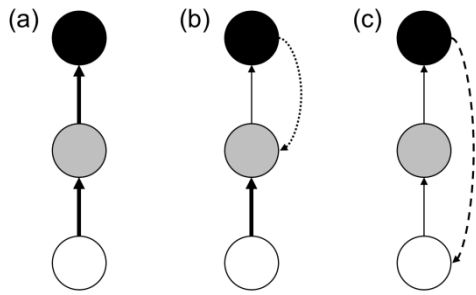
Figure 1: Different interaction topologies in a tritrophic system (**a**) **Trophic cascade**: Predators (black) eat herbivores (grey) which feed on plants (white). (**b**) **Non-consumptive effect**: Predators induce changes in traits (e.g. enhanced antipredator behaviour) of herbivores (dotted line). (**c**) **Trait-mediated indirect effect**: Changes in traits of herbivores from predators (e.g. reduced feeding behaviour) in turn affect plants (dashed line). Straight arrows point toward consumers and thickness of the solid lines indicates the strength of trophic links (After Schoener and Spiller 2012).

The endpoints of such trophic ladders depend largely on the chain length: odd numbers of trophic levels are expected to result in herbivore suppression and enhance plant performance. In contrast, even numbers of trophic levels enhances herbivores and plats are doing badly (Oksanen *et al.* 1981; Polis and Strong 1996). In a four level grassland cascade both functional top-predators (spiders) and risk spiders (spiders with glued mouthparts) reduced densities of intermediate predators which in turn enhanced herbivores (e.g. plant- and leafhoppers) (Schmidt-Entling and Siegenthaler 2009). So far, trait-mediated effects have mostly been studied in a two- or three-level trophic chain (Peacor *et al.* 2012; Forbes and Hammill 2013). Such linear trophic cascades are more an exception than the rule in nature: generalist predators prey on a variety of species (Polis 1991; Strong 1992). Moreover, they interact with other predators through competition or intraguild predation (Polis *et al.* 1989). Similarly, herbivores are often able to feed on various plant species and feeding on various trophic levels (i.e. omnivory) is common (Polis and Strong 1996). Therefore, cascades should be perceived as **interaction webs** rather than ladders to reflect natural complexity (Borer *et al.* 2005; Ohgushi 2005). Such interaction webs include both trophic links (food web) and trait-mediated links.

From wet to dry ecosystems

Trophic cascade theory predicts strong and far-reaching effects of predators on lower trophic levels (Hairston *et al.* 1960; Rosenzweig 1973; Oksanen *et al.* 1981). Due to the relative rarity and wide range of predators (compared with prey), empirical examination or cascade effects

proved to be rather difficult (Terborgh and Estes 2010). For practical reasons, **trophic cascades** have mostly been studied in aquatic ecosystems. The removal of 'keystone species' or 'whole lake experiments' revealed strong top-down control in aquatic ecosystems (Paine 1966; Carpenter *et al.* 1985). Several meta-analyses aimed at comparing the relative strength of trophic cascades among ecosystems conclude that effect sizes of predator on plant community biomass are higher in aquatic than in terrestrial ecosystems (Bigger and Marvier 1998; Borer *et al.* 2005; Gruner *et al.* 2008). They further conclude that invertebrate herbivores exert higher reduction of plant biomass than vertebrates. Ecologists suggested that top-down control is weaker in the more diverse terrestrial ecosystems comprising more complex food webs (Strong 1992). However, two recent meta-analyses demonstrated that trophic cascades can be at least as strong in terrestrial as in aquatic systems (Schmitz *et al.* 2000; Halaj and Wise 2001). The systematic study of **trait-mediated effects** is relatively younger compared to the classical density-mediated cascade studies. It boosted in the nineties based on the key review by Lima and Dill (1990) and the formulation of theoretical frameworks and terminology by Abrams (1995). Recent studies indicate that trait-mediated effects are equally important or can even exceed trophic effects on community dynamics (Preisser *et al.* 2005; Trussell *et al.* 2006a; Werner and Peacor 2006). Regarding ecosystem types the bias towards aquatic studies becomes even more eminent: more than 90 % of the studies included in the meta-analysis by Preisser and Bolnick (2008) were conducted in aquatic systems.

Research questions

The examination of the following research questions should contribute to fill current knowledge gaps about non-consumptive effects in terrestrial ecosystems. In this process, following aspects were addressed: (1) the occurrence of behavioural changes under spider predation risk; (2) identification of traits that determine the strength of antipredator behaviour; (3) fitness consequences of antipredator response; (4) effects of spider and ant predation risk on plant choice; (5) spider long-distance dispersal in relation to ant cues; (6) risk effects of spiders on arthropod communities and herbivory in the field.

(1) *How widespread are behavioural changes among terrestrial arthropods in response to spider cues?*

Spiders are a most diverse and abundant predacious arthropod group and they play a key role in terrestrial ecosystems by killing mainly insects but also other spiders (Wise 1993; Nentwig 2013). So far, behavioural responses to spider predation risk have only been studied among few arthropod groups. We were interested in the occurrence of behavioural changes in response to spider cues among arthropod species of a wide taxonomic range. We confronted 13 insect and eight spider species with cues of three common spider species in two different experimental setups. In the 'no-choice experiment', prey individuals were either put on filter papers bearing spider cues or on cue-free filter papers. In the 'choice experiment', prey individuals were allowed to choose between cue-bearing and cue-free filter paper halves. We quantified prey behaviour applying automated video analysis.

(2) *Which species traits determine the strength of antipredator behaviour in crickets?*

In the previous experiment, crickets repeatedly exhibited behavioural changes in response to spider cues. Here, we wanted to identify species traits of spiders that determine the strength of antipredator response in crickets. Thus, we confronted wood crickets (*Nemobius sylvestris*) with cues of 14 syntopic spider species using similar methods as described above. The selection of spider species allowed us to test for effects of various traits including predator hunting mode, predator commonness, predator diurnal activity and predator-prey body size ratio. Moreover we were interested in the direction of antipredator behaviour during the life cycle of the wood cricket and the nursery web spider (*Pisaura mirabilis*).

(3) *How are fitness components affected by spider predation risk?*

Behavioural changes under predation risk aim at a higher survival rate of prey (Lima and Dill 1990). We tested if experienced crickets are more successful in avoiding spider predation than crickets without previous exposure to spider cues. Because threatened herbivores are expected to reduce foraging (Lima and Bednekoff 1999), we quantified herbivory and weight gain of crickets under predation risk of the nursery web spider (*Pisaura mirabilis*). Furthermore, we were interested in the persistence of chemical spider cues. Therefore, we confronted crickets with spider cues of different age.

(4) *Does predation risk of spiders and ants affect plant choice and herbivory by crickets?*

Similar to spiders, ants play a pervasive role in terrestrial ecosystem by shaping prey communities and by interfering with other predators (Sanders *et al.* 2011). In this experiment, groups of crickets were allowed to choose between plants bearing predator cues and cue-free plants. A factorial combination of treatments allowed us to compare the relative strength of non-consumptive effects between spiders and ants. Thereby, we quantified plant choice, herbivory and weight gain of crickets in response to predation risk of spiders and ants.

(5) *Can ant chemical cues induce long-distance dispersal in spiders?*

So far, we investigated small scale movement in response to predator cues. Juvenile spiders in particular, but also adults of some spider families are capable to passively disperse through the air, termed as 'ballooning': Spiders release a thread of silk into the air and under suitable wind conditions they are carried away over hundreds of meters (Bell *et al.* 2005). We examined the dispersal propensity of juvenile spiders in response to ant chemical cues.

(6) *Does predation risk of spiders change arthropod communities and herbivory in the field?*

To complete our picture of trait-mediated effects in terrestrial ecosystems, we studied changes in arthropod communities and herbivory under spider predation risk in the field. Our new experimental approach allowed for natural colonisation of cue-bearing and cue-free plants during the experiment. Due to possible cue degeneration, we renewed spider cues every three days. We measured herbivory during the experimental period and analysed arthropod community at the end of the experiment.

Chapter 2

Effects of spider cues on arthropod behaviour

Roman Bucher, Hellena Binz, Florian Menzel and Martin H. Entling

The content of this chapter has already been published in an international peer-reviewed journal and can be accessed via the following reference and web link:

Bucher R, Binz H, Menzel F & Entling MH (in press) Effects of spider chemotactile cues on arthropod behavior. *Journal of Insect Behavior*, doi 10.1007/s10905-014-9449-1.

[Access]

Chapter 3

Influence of species traits on the strength of antipredator behaviour in crickets

Hellena Binz, Roman Bucher, Martin H. Entling and Florian Menzel

The content of this chapter has already been published in an international peer-reviewed journal and can be accessed via the following reference and web link:

Binz H, Bucher R, Entling MH & Menzel F (2014) Knowing the risk: crickets distinguish between spider predators of different size and commonness. *Ethology* 120:99-110.

[Access]

Chapter 4

Short-term fitness consequences of spider predation risk in crickets

Roman Bucher, Hellena Binz, Florian Menzel and Martin H. Entling

The content of this chapter has already been published in an international peer-reviewed journal and can be accessed via the following reference and web link:

Bucher R, Binz H, Menzel F & Entling MH (in press) Spider cues stimulate feeding, weight gain and survival of crickets. *Ecological Entomology*, doi 10.1111/een.12131.

[Access]

Chapter 5

Plant choice and herbivory of crickets in relation to spider and ant cues

Roman Bucher, Hannah Heinrich and Martin H. Entling

Abstract

Predators can indirectly reduce herbivory by killing herbivores. In addition, predation risk can influence feeding rate and feeding location. Herbivores are expected to avoid plants previously occupied by a predator. Consequently, less herbivory is expected on plants bearing predator cues. We examined if wood crickets, *Nemobius sylvestris* Bosc (Ensifera: Gryllidae), avoid plants bearing chemical cues of nursery web spiders, *Pisaura mirabilis* Clerck (Araneae: Pisauridae), or red wood ants, *Formica rufa* Linnaeus (Hymenoptera: Formicidae). Moreover, we were interested in the relative strength of risk effects among these two predators. We conducted a series of behavioural experiments, where crickets had the choice between a *Pisaura*/Control, *Formica*/Control, *Pisaura*/*Formica* and Control/Control plant. In addition, we quantified herbivory, the position of the crickets and weight change of crickets during the experimental period. Crickets strongly avoided plants with *Pisaura* cues. Correspondingly, herbivory was significantly reduced on these plants. Crickets showed no significant avoidance of ant cues, but the *Pisaura*-effect became non-significant if the alternative plant had been previously occupied by ants. Thus, ant cues played a weak role in plant choice. When wood crickets have a choice, predator cues lead to a shift of herbivory towards cue-free plants rather than to an overall reduction in plant damage that is expected if predators prey on herbivores.

Introduction

Predators can play a key role in ecosystems by controlling lower trophic levels (Paine 1966; Estes *et al.* 1998; Schmitz *et al.* 2000). Density-mediated effects of predators such as killing the prey have been the main focus of top-down control (Hairston *et al.* 1960; Rosenzweig 1973; Oksanen *et al.* 1981). In addition, prey individuals often perceive predators by chemical cues (Kats and Dill 1998). This allows prey individuals to reduce predation rate by changing characteristic traits such as morphology, physiology, and behaviour (Lima and Dill 1990; Raimondi *et al.* 2000; Slos and Stoks 2008). Escape and hiding behaviour for example enhances prey survival but comes at a cost: hiding behaviour or death feigning reduce the time spent feeding and therefore reduce food intake (Lima and Dill 1990). Additional movement or increased activity is likely to be energy demanding as well (Ydenberg and Dill 1986).

Foraging behaviour in response to predation risk is of particular interest, because it affects biomass uptake of herbivores. Changes in herbivory under predation risk can occur in two ways. First, predator cues induce changes in the feeding rate (e.g. due to altered energy demands; Hawlena and Schmitz 2010) or in the time spent feeding of herbivores (e.g. increased vigilance; Lima and Dill 1990). Second, herbivores avoid plants previously occupied by a predator, which reduces local herbivory but may increase herbivory elsewhere (Schmitz *et al.* 1997). In the latter case, predation risk affects local herbivore density even if no herbivores are killed by the predator (Pearson 2010). Trait-mediated indirect effects are risk effects of predators that cascade down to primary producers via changes in traits of intermediate species (e.g. feeding behaviour of herbivores) (Abrams 2007), and can even exceed density-mediated effects (Schmitz *et al.* 2004; Preisser *et al.* 2005). Risk effects of predators can indirectly affect ecosystem functions such as herbivory (Beckerman *et al.* 1997), nutrient cycle (Hawlena *et al.* 2012), and plant community composition (Schmitz 2003).

Many terrestrial studies used spiders as predators to investigate predator effects on arthropod prey (Schmitz 1998). In addition, ants play a pervasive role in terrestrial ecosystems by killing herbivore/omnivore prey (Vandermeer *et al.* 2002; Piñol *et al.* 2012), but also by interfering with other predators (Sanders and Platner 2007; Mestre *et al.* 2014). Similar to spiders, ant chemical cues can influence prey behaviour (Rudgers *et al.* 2003; Oliver *et al.* 2008), and in turn protect plants (Messina 1981). The relative strength of spider *versus* ant

trait-mediated effects, however, remains unknown. Moreover, it is questionable if predation risk of multiple predators leads to higher fitness costs than risk of only one predator species.

We examine effects of predator cues on plant choice, foraging behaviour and weight gain in crickets. Predator cues consist of chemical cues of spiders and ants (e.g. faeces droplets, chemical footprints and/or dragline silk). Former studies demonstrated that crickets, in particular, show strong behavioural response if confronted with cues of different spider species (Kortet and Hedrick 2004; Storm and Lima 2008; Binz *et al.* 2014; Bucher *et al.* in press-a). We conducted a series of plant choice experiments to quantify the position of the crickets, herbivory, and weight change of crickets. The experimental design allows us to compare the relative strength of trait-mediated effects between the two predators and the combined effect of both predators. We expect 1) that crickets avoid plants bearing predators cues, 2) reduced herbivory on cue plants compared with control plants, 3) lowest overall herbivory, and 4) lowest weight gain of crickets in the presence of chemical cues of both predators.

Materials and Methods

Study species

All species were collected in a mixed forest near Bellheim (49°11'45" N / 8°19'08" E) (Rhineland-Palatinate, Germany) between April and June 2013. Woodland strawberry plants, *Fragaria vesca* Linnaeus (Angiosperms: Rosaceae), were planted into small cups and held in a climatic chamber at 25°C and 75% humidity for at least three days prior to the cue preparation. Natural day/night rhythm (L12:D12) was simulated using fluorescent lamps (OSRAM L 58W/77 Fluora). We only used strawberry plants without any visible leaf damage. Wood crickets, *Nemobius sylvestris* Bosc (Ensifera: Gryllidae), and nursery web spiders, *Pisaura mirabilis* Clerck (Araneae: Pisauridae), were collected by hand. Red wood ants, *Formica rufa* Linnaeus (Hymenoptera: Formicidae), were collected directly from the surface of a nest. Crickets and ants were maintained in groups in plastic terraria (30 x 20 x 20 cm). The sidewalls were covered with Fluon to prevent escape of insects. Crickets were fed with apple and carrots *ad libitum*, ants were fed with honey and dead crickets (*Acheta domesticus* Linnaeus). Crickets were starved for one week prior to the experiments. Nursery web spiders were maintained singly in 40ml glasses and fed with fruit flies (*Drosophila hydei* Sturtevant) twice a week to keep them on an intermediate hunger level. We only used adult female spiders, because males stop hunting once they reach adulthood (Foelix 2011).The

animals were held in a climatic chamber at 16°C and 65% humidity and L12:D12 light rhythm.

Cue preparation

Three days before the experiments we standardized strawberry plants to three intact leaves by removing additional leaves, flowers and fruits. The strawberry plants were transferred to petri dishes (9 cm in diameter) filled with dried sandy soil from the animal collection site. Our treatments were either a nursery web spider or five red wood ants on plants. Our controls were plants with neither a spider nor ants. We had ten *Pisaura* plants, ten *Formica* plants and 20 control plants per experimental cycle. We covered all plants with plastic cups (height: 10.5 cm, diameter bottom: 7.25 cm, diameter top: 10 cm). The inner surface of the plastic cups was covered with Fluon to force spiders and ants to stay on the plants. The Petri dishes and plastic cups were connected with Parafilm (BEMIS Company, Neenah, USA) to prevent escape of spiders and ants. After three days of cue deposition, all animals were removed. Two plants were assigned to a terrarium (30 x 20 x 20 cm) with a 1.5 cm layer of sandy soil. The middle line between the plants was marked with a woody stick. The assortment of the plants led to four different treatment combinations (among 20 terraria): *Pisaura*/Control, *Formica*/Control, *Pisaura/Formica,* and Control/Control. Each treatment combination was replicated five times per experimental cycle. In total, we performed five experimental cycles (with maximal two weeks between the cycles) ending up with 25 replicates per treatment combination. For every experimental cycle we used new strawberry plants, crickets and ants. Nursery web spiders were partly reused for cue deposition.

Experimental procedure

Prior to the experiments, we measured the weight of each cricket. We then added a group of five crickets to each terrarium and covered the terraria with plastic film. For the next three days, we noted the location of the crickets (plant choice: number of crickets on each side of the terrarium; position: number of crickets on plants *versus* on the ground) three times a day (9 am, 1 pm, and 5 pm). We stopped the experiments on day four, after a last observation. We reweighted the crickets and quantified herbivory on the strawberry leaves. To quantify leaf damage, we scanned the leaves (CANON CanoScanLiDE 110) and used the program ImageJ (Rasband 2011) to measure the leaf area that has been consumed by crickets.

Data analysis

To test for plant choice in relation to the presence of predator cues, we pooled the observations over the three days of each experimental run. We calculated a generalized linear model with quasi-binomial error distribution to compare the proportion of crickets between both sides of each terrarium for the three treatment combinations (*Pisaura* cues only, *Formica* cues only, and cues of both predators). Similar to the plant choice analysis, differences in herbivory between the two plants in each terrarium were compared for the three treatment combinations using a linear model. The repeated observations of cricket position (ground *versus* plant) were again pooled over the three days of each experiment. The proportion of crickets on plants was compared between the three treatment combinations and the control by calculating a generalized linear model with quasi-binomial error distribution. To compare total herbivory between the treatment combinations and the control, we calculated a generalized model following gamma error distribution. Mean weight change of crickets per terraria was compared using a linear mixed model. Because weight gain increased during the whole experimental period, the experimental cycles entered the model as a random effect with correlation structure (e.g. consecutive cycles are more similar). All statistical analyses were done in R Version 2.14.1 (R Development Core Team 2011).

Results

Plant choice and herbivory

Crickets avoided *Pisaura* plants and preferred the control side of the terraria (Fig. 1A; t_{24} = -2.17, P = 0.033). However, preferences were similar between control and *Formica* plants (t_{24} = -1.47, P = 0.15) and between *Pisaura* and *Formica* plants (t_{24} = -1.1, P = 0.28). In accordance with the plant choice results, herbivory was higher on control plants compared with plants bearing *Pisaura* cues (Fig. 1B; t_{24} = -2.6, P = 0.010). Again, no significant differences were detected among the remaining treatment combinations (Control/*Formica*: t_{24} = -0.26, P = 0.80; *Formica*/*Pisaura*: t_{24} = -0.62, P = 0.54).
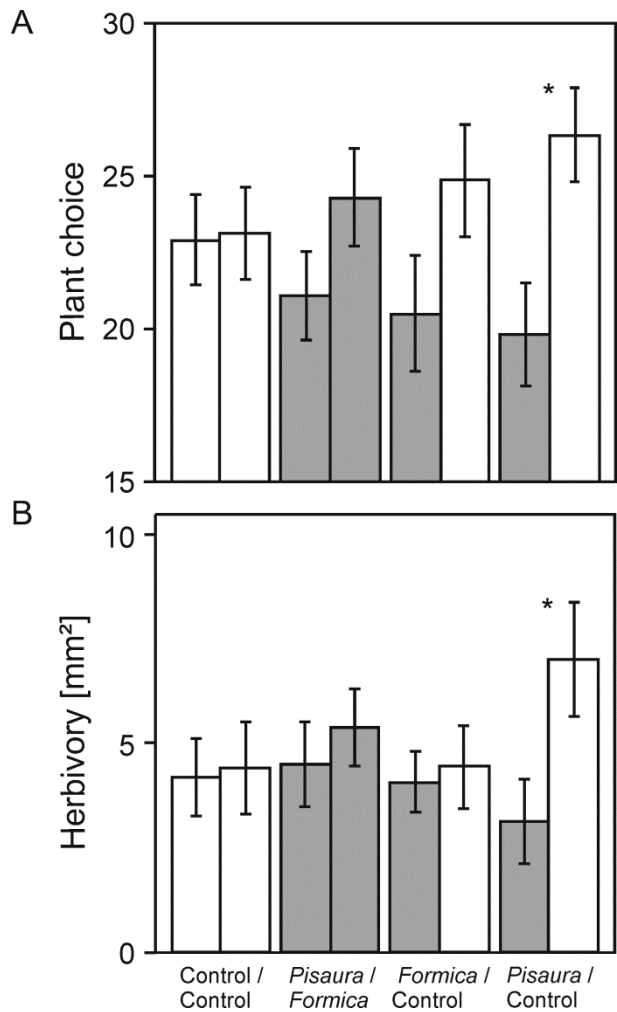
Figure 1: (**A**) Plant choice of crickets among the four treatment combinations. Grey bars represent observations of crickets on plants bearing predator cues; white bars represent crickets on control plants. If crickets had the choice between a plant bearing *Pisaura* cues and a control plant they were more often observed on the control side (* P < 0.05). Preferences were similar among the remaining treatment combinations. (**B**) Reduced herbivory on *Pisaura* compared with control plants (* P < 0.05). Herbivory was similar among the remaining treatment combinations.

Cricket position, overall herbivory and weight gain

Treatment combinations did not affect the position of crickets on ground *versus* plants (Fig. 2A; $\chi^2_{3,96}$ = 4.43, P = 0.22). However, in terraria with a *Pisaura* and a control plant, crickets were more often observed on the ground than on the plants compared with the control terrarium (t_{24} = 2, P = 0.048). Cricket position did not differ between the remaining treatment combination and the control terraria (two control plants) (Control/*Formica*: t_{24} = 1.38, P =0.17; *Formica*/*Pisaura*: t_{24} = 1.3, P = 0.20). Total herbivory by crickets did not differ among the treatment combinations (Fig. 2B; $F_{3,96}$ = 0.35, P = 0.79). Treatment combinations were similar to control terraria (Control/*Pisaura*: t_{24} = -0.75, P = 0.46; Control/*Formica*: t_{24} = 0.052, P = 0.96; *Formica/Pisaura*: t_{24} = -0.63, P = 0.53). Overall, the treatment combination did not affect weight gain of the crickets (Fig. 2C; $F_{3,96}$ = 0.99, P = 0.40). Crickets tended to gain less weight in the presence of cues of both predators compared with the control terraria (t_{24} = -1.7, P = 0.091), with intermediated weight gains in the presence of cues from one predator species alone (Control/*Pisaura*: t_{24} = 0.86, P = 0.39; Control/*Formica*: t_{24} = 1.07, P = 0.29).
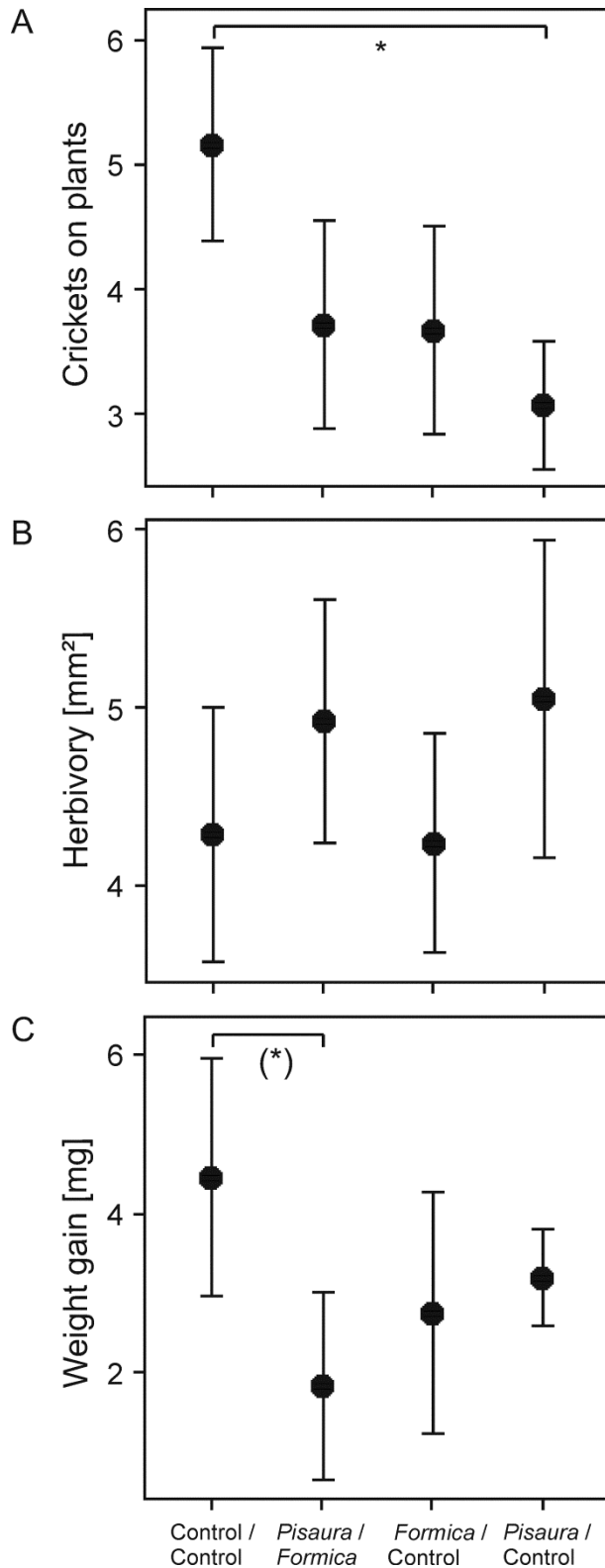
Figure 2: (**A**) Mean number of crickets observed on the plant. Crickets preferred to stay on the ground (cue free zone) in terraria containing a plant with and without *Pisaura* cues compared with terraria containing plants without any predator cues (* $P < 0.05$). There was no significant plant avoidance in the presence of a *Formica* plant or of two plants bearing cues of both predators. (**B**) No significant differences in total herbivory (herbivory on both plants within a terrarium) among the four treatment combinations. (**C**) Mean weight gain of crickets among the four treatment combination. Crickets tended to gain less weight in the

presence of cues of both predators compared with the control ((*) P < 0.1). Weight gains were similar between the control and the presence of cues of either of the two predators.

Discussion

In accordance with our hypothesis, crickets strongly avoided strawberry plants bearing *Pisaura* cues and frequented cue-free control plants more often. Wood crickets repeatedly change their behaviour in response to *Pisaura* chemotactile cues (Binz *et al.* 2014; Bucher *et al.* in press-a). These previous behavioural experiments were conducted on filter papers with and without spider cues. The method applied in this study poses a more natural situation and suggests that crickets avoid plants previously occupied by spiders in the field. Ant cues on the other hand did not significantly influence plant choice if crickets could choose between a control plant and a plant bearing ant cues. In the presence of cues of both predators, the avoidance of plants bearing *Pisaura* cues became non-significant. This indicates that ant cues also deter crickets, but less so than *Pisaura* cues. The different impact of these two predators on crickets can be explained by their relative threat: *Pisaura* spiders show high acceptance towards crickets as prey (Nentwig and Wissel 1986). By comparison, interference between crickets and ants may only play a subordinate role on the forest ground. Relatively low aggression of *Formica* ants towards wood crickets was revealed by personal observations in the field and by confrontation experiments in the lab (Elena Franziska Kraft, unpublished data).

Similar to the preference for control plants, crickets were more often observed on the ground than on plants in the presence of at least one plant bearing predator cues. But again, changes in the position of crickets were only significant in the presence of a plant bearing *Pisaura* cues. The shift in microhabitat use from plants towards the ground may reduce predation risk by *Pisaura* spiders, which prefer to hunt on the vegetation (Roberts 1996). *Formica* ants induced weaker predator avoidance. They can reach high densities on the ground, but also climb in the vegetation (Jacobs *et al.* 1998). Thus, we would not expect a strong shift in cricket position in response to ant cues.

The herbivory pattern matches the plant choice results: reduced herbivory on strawberry plants bearing *Pisaura* cues compared with control plants. Similar to the plant choice results, we found no significant differences in herbivory in relation to ant cues. Plant choice under predation risk of *Pisaura* spiders affected herbivory in this study. In a previous microcosm experiment, we forced crickets to stay on strawberry plants bearing cues of *Pisaura* spiders (no alternative cue-free plant; Bucher *et al.* in press-b). In this 'no-choice

experiment', we found a tendency towards increased herbivory in the presence of *Pisaura* cues indicating that crickets compensate energy costs through enhanced feeding, while hiding between plant leaves. In this case, predators indirectly enhanced herbivory. When we offered the crickets a control plant, predation risk did not affect overall herbivory, but it led to a shift in herbivory towards the control plants. This is in accordance with the classic Beckerman et al. (1997) field experiment, where grasshoppers moved to safer locations (more complex vegetation structure), which reduced herbivory on grasses but increased herbivory among herbs. Thus, spider predation risk induced two opposing cascade effects that did not result in a net effect on herbivory (Halaj and Wise 2001). If we consider nature as a 'landscape of fear' with areas of high and low predation risk (Brown *et al.* 1999; Schmitz *et al.* 2004; Laundré *et al.* 2010), herbivory should not change substantially if organisms have the chance to move to safe locations. Instead, total herbivory should be redistributed from high risk locations to low risk locations. Thus, as long as predator densities are low enough to only partly occupy a habitat, we hypothesize that herbivory becomes more heterogeneously distributed (see Polis 1999) instead of overall reduced through trait-mediated effects.

In the presence of cues from both predators, crickets gained the least weight, although we could not detect any differences in overall herbivory among the treatment combinations. The presence of cues of either of the two predators did not affect weight gain compared with crickets in control terraria. The conversion of consumed leaves into storage metabolites may be reduced only in the presence of both predators. However, additional experiments would be necessary to test if this is an effect of predator (cue) diversity or because both plants in the respective arenas carried predator cues (cue quantity).

Our lab experiment revealed avoidance of plants bearing spider cues, which in turn reduced leaf damage by crickets. On the contrary, ant cues played only a subordinate role in terms of plant choice and differences in herbivory. The offer of two alternative plants yielded different results compared with an earlier 'no-choice experiment'. This demonstrates that the revealed aspects of herbivore response to predation risk depend on the complexity of the experimental setting. Shifts in local herbivory in the presence of predator cues highlight the importance of spatial dynamics in trait-mediated effects. Local trait-mediated indirect effects did not result in a net change of herbivory that is expected if predators kill prey. Instead, they increased spatial heterogeneity of herbivory.

Chapter 6

Effects of ant cues on the long-distance dispersal of spiders

Laia Mestre, Roman Bucher and Martin H. Entling

The content of this chapter has already been published in an international peer-reviewed journal and can be accessed via the following reference and web link:

Mestre L, Bucher R & Entling MH (2014) Trait-mediated effects between predators: ant chemical cues induce spider dispersal. *Journal of Zoology* 293:119-125.

[Access]

Chapter 7

Impact of spider predation risk on arthropod communities and herbivory
in the field

Roman Bucher, Florian Menzel and Martin H. Entling

Abstract

Food web theory suggests that predators can indirectly enhance plant performance via herbivore suppression. In addition to prey consumption, changes in prey traits (e.g. avoidance behaviour) can contribute to the reduction in herbivory. We performed a field experiment to determine the extent of such non-consumptive effects towards adjacent trophic levels. We repeatedly enclosed spiders (*Pisaura mirabilis*) on plants (*Urtica dioica*) for cue deposition. Control plants were enclosed in the same way but without spiders. After cue deposition, the enclosures were removed to allow arthropods to colonise the plants and feed on them. At the end of the herbivory experiment, the arthropods were sampled to determine community composition. The presence of chemotactile spider cues reduced leaf damage by 50 %. In addition, spider cues led to changes in the arthropod community: smaller spiders avoided plants with spider cues. In contrast, the aphid-tending ant *Myrmica rubra* showed higher recruitment of workers on cue-bearing plants, possibly to protect the aphids. Our results show that the risk of spider predation can reduce herbivory on nettles. They further demonstrate that non-consumptive effects can be particularly strong within the predator guild.

Introduction

Predators influence prey populations by killing prey individuals. These 'density-mediated effects' have long been recognized as a main driver in predator-prey dynamics (Hairston et al. 1960). Due to the strong selective pressure of predation, prey individuals evolved various strategies to avoid predation (Werner and Peacor 2003). Predator effects other than eating prey (consumptive effects) have been named 'non-consumptive effects' or 'trait-mediated effects' (Abrams 2007). They occur if prey organisms change characteristic traits such as morphology, reproductive strategy, or behaviour in response to predation risk. For example, pea aphids (*Acyrthosiphon pisum*) confronted with adult ladybirds (Coccinellidae) increase the production of winged females that are able to move to potential enemy-free locations (Weisser et al. 1999). In contrast, fall field crickets (*Gryllus pennsylvanicus*) reduce their mobility in the presence of chemotactile cues of the wolf spider *Tigrosa helluo*, probably to reduce the chance of being detected by the predator (Storm and Lima 2008). Changes in species traits enhance predator avoidance but come at a cost: reduced mobility or hiding behaviour for example can reduce the time available for foraging (Lima and Dill 1990). Thus, individuals are expected to balance predator avoidance with the incurred fitness costs (Sih 1980; Lind and Cresswell 2005).

According to the trophic cascade theory, effects of predators on prey can be transmitted to lower trophic levels. Top-down trophic cascades play a central role in the so called 'green world hypothesis' (Hairston et al. 1960). It proposes that predators directly suppress prey (i.e. primary consumers). In doing so, predators indirectly release producers from herbivory and thereby enhance biomass accumulation (but see White (1978) for an alternative bottom-up approach). Although trophic cascade theory originated from aquatic systems, recent studies revealed evidence for top-down trophic cascade effects in terrestrial ecosystems (Schmitz *et al.* 2000; Halaj and Wise 2001). Non-consumptive effects are important determinants of population and community dynamics and often act in concert with consumptive (trophic) effects (Polis 1994). These early ideas of trophic cascades have led to the concept of trait-mediated indirect effects, where actions of one species (e.g. a predator) to another (e.g. a plant) are transmitted via a change in the trait of an intermediate species (e.g. feeding behaviour of a herbivore) (Abrams 1995). Recently, it has been shown that trait-mediated indirect effects play a pervasive role in terrestrial ecosystems by influencing herbivory, diet, nutrient dynamics, and finally plant community composition (Beckerman *et al.* 1997; Schmitz 2003; Schmitz *et al.* 2010; Hawlena *et al.* 2012).

In this study, we were interested to which extent spider non-consumptive effects on arthropods affect plant performance in the field. To distinguish between non-consumptive and consumptive effects, predators must be prevented from killing prey. To simulate predation risk, we therefore enclosed spiders on plants for the deposition of chemotactile cues (i.e. faeces, chemical footprints and/or dragline silk), but removed them for the actual experiment. We hypothesized that (1) herbivory would be reduced on plants with spider cues, and (2) that the arthropod communities on plants with spider cues would differ from those of cue-free plants.

Methods

Field site and study species

The field study was conducted in a semi-natural grassland on the Ebenberg, Germany (49°11'03"N/8°07'51"E) between early-May and mid-June 2013. This former military training site has not been used for agriculture since the 19th century and covers an area of 225 hectares. It consists mainly of dry grassland on sand-loess soil, interrupted by hedges and single standing trees. With an average temperature of 12 ± 0.67 °C and an average humidity of 93 ± 1.65 % (with 100% humidity in 23 out of 43 days), the weather in the experimental period was relatively cool and wet.

As cue donator, we used nursery web spiders (*Pisaura mirabilis*). This relatively large spider induced behavioural changes in previous studies (Binz *et al.* 2014; Bucher *et al.* in press-a). Adult females were collected manually at the study site. We chose stinging nettles (*Urtica dioica*) to quantify herbivory in relation to presence/absence of *Pisaura* cues. First of all, nettles have a wide geographical distribution and provide the habitat for a diverse arthropod community (Davis 1989). Secondly, *Pisaura* spiders can show high densities among nettle plants and frequently hunt on nettle leaves (RB, personal observation).

Field methods

Individual nettle plants were attached to a bamboo stick (1.5 m tall and 1.5 cm thick). At the beginning of the experiment nettle plants measured a total height of 57 ± 1.1 cm and 99.5 ± 1.6 cm at the end. One adult female *Pisaura* was enclosed on each of N = 30 single nettle shoots using cylindrical enclosures (black plastic insect mesh with 1 mm mesh size; 1 m tall and 20 cm in diameter). The mesh tube was closed around the stem close to the ground as well as above the nettle plant. Thirty control plants were enclosed in the same way, but

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without spider. The treatments were randomly assigned among the nettle population. All experimental plants were separated by at least 1 m from each other. Spiders were put on the plants for three days for cue deposition. Afterwards the meshes and spiders were removed to allow arthropods to colonise the plants and feed on the nettle leaves. Most previous experiments about effects of spider predation risk (i.e. disabled spiders) on herbivores and plants employed completely enclosed cages (Beckerman *et al.* 1997; Schmitz *et al.* 1997; Schmitz 1998). This practice has been criticized because such cages exclude alternative prey as well a natural enemies of spiders and can thus yield unnaturally high cascade effects and an overestimation of these effects (Halaj and Wise 2001). Spider cues decay within a relatively short time period (Wilder *et al.* 2005; Bucher *et al.* in press-b). Therefore, we renewed the spider cues after another three days. All arthropods on the plants were removed with a vacuum sampler (modified STIHL SH68, Stihl, Waiblingen, Germany) to prevent that spider consumption could take place. Then, the spider and the control enclosures (respectively) were again applied to the plants. For the herbivory measurement, we repeated this procedure seven times (experimental cycles) during 30 days.

To measure herbivory, we marked three leaves per nettle plant with colourful strings. Before the experiment and after every experimental cycle, we took standardized pictures (CANON EOS 400D with a 60 mm Macro lens on a millimetre scale background) of the marked leaves. After the first cycle, three additional, newly grown leaves were marked. In total, herbivory on six leaves per plant was tracked over 15 days (the experiment lasted 30 days but only half of the time arthropods were able to feed on the leaves). To screen for shifts in arthropod colonization, we sampled the arthropod community after an additional cue deposition. Spiders were removed at 8 am and arthropods that colonised the plants during the day (12 h) were obtained with suction sampling.

Data analysis

To quantify herbivory, we compared the pictures of individual leaves from the beginning of the experiments with those at the end of the experimental period. The leaf area eaten during the experimental period was measured using the software ImageJ version 1.45s (Rasband 2011). The effect of *Pisaura* chemotactile cues on leaf herbivory was estimated using a Generalized Linear Mixed Model (GLMM) with gamma error distribution. The individual nettle plant entered the model as random effect to account for variation among the individual plants using penalized quasi-likelihood method (Zuur 2009). Linear Models (LM) revealed that plant size did not differ between the two treatments, neither at the beginning ($F_{1,58} = 0.36$,

$P = 0.55$; plant height: 57 ± 1.1 cm) nor at the end of the experiment ($F_{1,58} = 1.33$, $P = 0.25$; plant height: 99.5 ± 1.6 cm).

Arthropods from the suction samples were identified to species level if feasible. Groups consisting of relatively few individuals (< 15) (e.g. some beetle families or different spider families) were combined on a lower taxonomic level (e.g. beetles and spiders) to increase statistical power. We used PERMANOVA from the 'vegan' package (Oksanen *et al.* 2013) to test for difference in arthropod communities in relation to the presence of spider cues. To test for treatment effects in each group separately, we used Generalized Linear Models (GLM) with quasi-poisson error distribution. To uncover relationships between the arthropod groups we calculated Pearson's correlation coefficients (see **Figure 3**). All statistical test were conducted in R version 2.14.1 (R Development Core Team 2011).

Table 1: Arthropod groups sampled from the nettle plants. N indicates the total number of individuals sampled. Differences in abundance between cue-bearing und control plants were obtained from generalized linear models following quasi-poisson distribution.

Group	Order	Family	Species	N	χ^2	*P*-value	
Insecta	Hemiptera	Triozidae	*Trioza urticae*	981	0.91	0.340	
		Aphididae	*Microlophium carnosum*	93	0.53	0.470	
		Cicadellidae	*Eupteryx urticae*	79	0.20	0.660	
			other species (juv.)	135	0.15	0.700	
	Heteroptera			22	0.18	0.670	
	Coleoptera	Apionidae	*Taeniapion urticarium*	23	0.04	0.840	
		Brachypteridae	*Brachypterus* sp.	17	0.04	0.830	
		other families		21	1.38	0.240	
	Diptera			148	1.06	0.300	
	Hymenoptera	Formicidae	*Myrmica rubra*	111	5.90	0.015	*
			Lasius niger	27	5.55	0.018	*
			other species	20	2.63	0.110	
		suborder Parasitica		34	2.91	0.088	(*)
Acari				30	1.96	0.160	
Araneae				16	5.58	0.018	*

Results

Herbivory on plants bearing spider cues was 49.5% lower compared to control leaves (**Figure 1**; $F_{1,58} = 97.6$, $P < 0.001$). On control leaves, herbivores removed 8.00 ± 1.6 mm² of 2902.89

± 232.87 mm² leaf area compared to only 4.04 ± 1.1 mm² of 2695.62 ± 221.06 mm² in the presence of spider cues. The main foliage-eating weevil (*Phyllobius pomaceus*) was largely missing in the arthropod sampling at the end of the experimental period. Instead, the sampled arthropod community on the nettles was dominated by the psyllid *Trioza urticae* (Hemiptera, Triozidae) (see **Table 1**), which feeds on punctured plant tissue comparable to aphids and thus cannot cause the herbivory that we measured as loss of leaf are (Hodkinson 1974). In addition, both partners of an ant-aphid mutualism were well represented in our arthropod sampling: the common red ant *Myrmica rubra* and the common nettle aphid *Microlophium carnosum*. Overall, arthropod communities significantly differed between the cue-bearing and cue-free plants (PERMANOVA: pseudo-$F_{1,57}$ = 1.76, P = 0.032). Surprisingly, the ant *Myrmica rubra* was more abundant on cue-bearing plants (**Figure 2**; $\chi^2_{1,58}$ = 5.9, P = 0.015). In contrast, the ant *Lasius niger* and spiders showed lower abundances on risk plants (**Figure 2**; *Lasius*: $\chi^2_{1,58}$ = 5.55, P = 0.018; Spiders: $\chi^2_{1.58}$ = 5.58, P = 0.018). Additionally, hymenopterans (exclusively belonging to the Parasitica suborder) showed a tendency towards lower abundances in the presence of *Pisaura* cues (**Figure 2**; $\chi^2_{1,58}$ = 2.91, P = 0.088). No difference was found for the remaining arthropod groups.
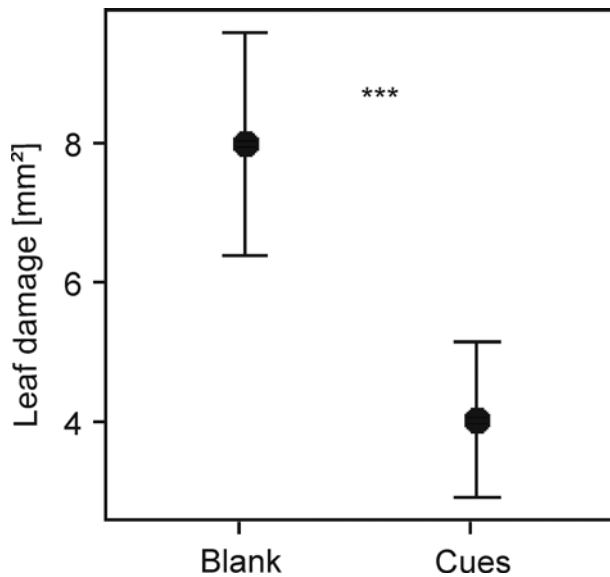

Figure 1: Herbivory on control plants compared to plants bearing spider chemotactile cues. Herbivory was almost 50 percent reduced on plants previously occupied by a nursery web spider (*** $P < 0.001$).
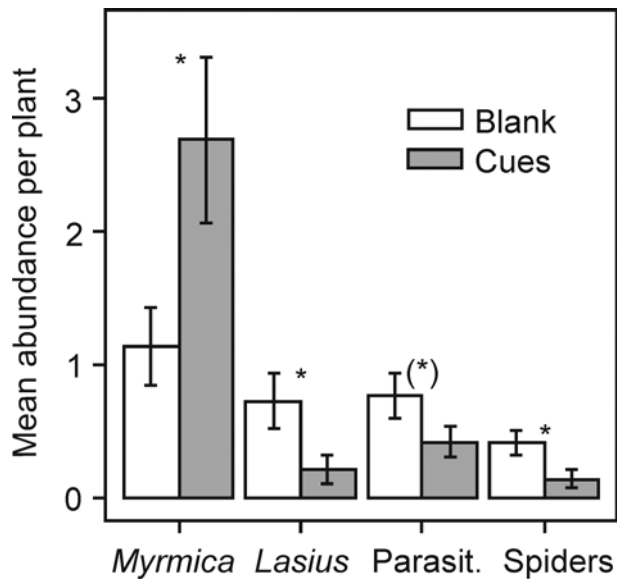
Figure 2: Mean abundance of the two most frequent ant species (*Myrmica rubra* and *Lasius niger*), parasitoid hymenopterans and spider on cue-bearing (grey) and control plants (white). The asterisks indicate significant differences in arthropod abundance between the treatments (* $P < 0.05$, (*) $P < 0.1$)

Discussion

In accordance with both hypotheses, risk of spider predation reduced herbivory and changed the arthropod community, particularly at the intraguild level. Herbivory on leaves bearing *Pisaura* cues was reduced by half, underlining that non-consumptive effects of spiders can have profound consequences for ecosystem functions. In accordance with our results, spiders with glued mouth parts or spider silk alone were sufficient to reduce herbivory in earlier studies (Beckerman et al. 1997; Rypstra and Buddle 2013). Thaler and Griffin (2008) found reduced plant damage by *Manduca sexta* (Lepidoptera) in the presence of both functional and disabled predators (*Podius maculiventris*, Heteroptera). In their study system, consumptive and non-consumptive components contributed equally to the reduction in herbivory. The leaf damage observed in our experiment would barely lead to changes in plant biomass, even if it was up scaled beyond the 15 days during which herbivory was recorded. Halaj and Wise (2001) showed that studies investigating trophic cascades in natural terrestrial ecosystems reveal only minor effects on plant biomass. Trophic cascades were stronger in species-poor agricultural ecosystems (Halaj and Wise 2001), suggesting that also non-consumptive effects of predators on herbivory may be stronger there.

Under predation risk (i.e. physiological stress see Stoks et al. (2005)), herbivores can compensate enhanced energy demands by increased uptake of energy-rich diet like

carbohydrates in grasshoppers (Hawlena and Schmitz 2010). Indeed, we found higher herbivory in response to *Pisaura* cues in small microcosms where wood crickets (*Nemobius sylvestris*) had no opportunity to switch to safe places or other food sources (Bucher *et al.* in press-b). However, when offered a choice between plants bearing *Pisaura* cues and cue-free control plants, the crickets strongly avoided risk plants (RB unpublished data), and in this case, no higher food uptake (e.g. due to stress) was measurable. We thus suggest that the reduced herbivory found in this study results from a shift of herbivores and/or omnivores to safer plant individuals or to other food sources.

Based on the feeding pattern and personal observations during the experiment, the quantified herbivory was almost exclusively caused by the weevil *Phyllobius pomaceus*. This particular weevil species is a main chewing herbivore on nettles (besides some caterpillar species that were missing on our plants at that time) and shows a short peak in their abundance in May (Davis 1973). Unfortunately, *Phyllobius pomaceus* were no longer present at the time of the arthropod sampling. During the field experiment we conducted some standardized behavioural arena experiments (see Binz *et al.* 2014) to test for behavioural changes in *Phyllobius pomaceus* in response to *Pisaura* chemotactile cues. We could not detect any changes in *Phyllobius* behaviour in response to *Pisaura* cues (RB, unpublished data). However, plant choice in response to spider cues may remain undetected in such simplified laboratory experiments. Alternatively, higher densities of *Myrmica* workers could have reinforced non-consumptive effects of *Pisaura*.

Surprisingly, the most frequent ant *Myrmica rubra* increased its abundance in the presence of *Pisaura* cues. We tentatively interpret this unexpected result as an increased recruitment of *Myrmica* workers to protect *Microlophium carnosum* aphids. *Lasius niger*, a less frequent visitor in our study system (**Figure 2**), was negatively affected by the presence of spider cues, possibly to avoid intraguild interference with *Pisaura* or *Myrmica* (see **Figure 3**). Relatively small spiders (from the Families of Araneidae, Linyphiidae, Philodromidae, Salticidae, Tetragnathidae, Theridiidae, and Thomisidae) avoided plants previously occupied by the larger *Pisaura*. For the smaller wolf spider *Pardosa milvina,* it has repeatedly been shown that they avoid the larger *Tigrosa helluo* based on chemotactile cues (Persons *et al.* 2001; Persons *et al.* 2002). Alternatively, spiders may have avoided cue-bearing plants due to the higher density of *Myrmica rubra*. Ants are well-known to influence arthropod communities on plants by predation and intraguild interference (Sanders and Platner 2007), and chemical ant cues can induce spider emigration (Mestre *et al.* 2014). In the same way, the tendency of lower spider densities could be due to shifts in ant community rather than to

avoid predation by *Pisaura* spiders. However, we found only weak negative correlations between *Myrmica* abundance and spiders or *Lasius niger* (see **Figure 3**). This indicates that changes in arthropod abundance are mainly due to the presence or absence of spider cues rather than due to the higher *Myrmica* density on cue plants. Further field experiments should therefore disentangle the relative importance of non-consumptive effects by spiders and ants.
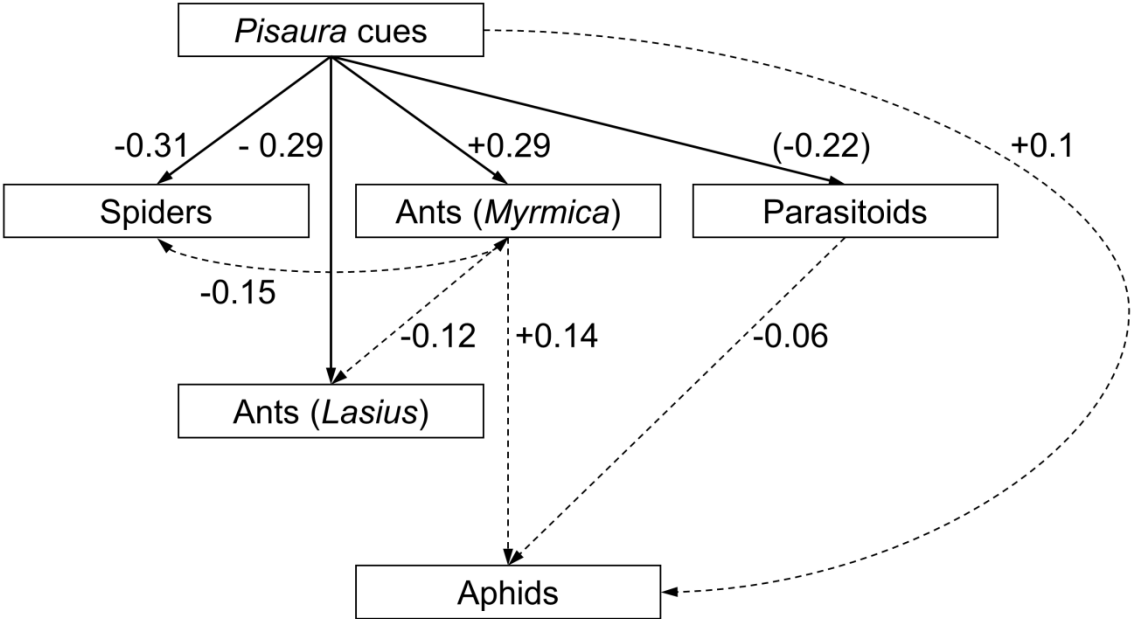

Figure 3: Interaction web on the nettle plants at the end of the field experiment. Numbers indicate standardized correlations coefficients. Solid lines indicate significant connections at the 0.05 level or a trend for the *Pisaura* cues-parasitoid relationship (p < 0.1). Dashed lines represent non-significant connections.

Our study demonstrates that the presence of chemotactile spider cues strongly reduces leaf damage by herbivorous insects. Moreover, our field experiment revealed changes in arthropod community in response to spider chemotactile cues, namely an enhanced recruitment of *Myrmica* workers, and decreased abundances of *Lasius niger* ants and spiders (and possibly parasitoid hymenopterans). As spiders and ants are ubiquitous, generalist predators (Sanders and Platner 2007), such trait-mediated intraguild interactions may have strong and far-reaching effects on the structure and function of terrestrial food webs. Although most studies concentrate on 'trophic ladders' (e.g. spider-grasshopper-plant) and do not take into account additional generalist top predators, intermediate predators, and/or alternative prey (Polis 1991; Strong 1992), the interplay of spiders and ants as shown here highlights the importance of incorporating interaction web structure in cascade analysis.

Chapter 8

Synthesis and outlook

Roman Bucher

Wood crickets – jack of all trades

Behavioural changes in response to spider chemotactile cues were relatively scarce among the tested species. However, wood crickets changed their behaviour in response to chemotactile cues of various spider species. This result is not surprising, as behavioural changes in the presence of spider cues have repeatedly been demonstrated for crickets (Kortet and Hedrick 2004; Storm and Lima 2008). Moreover, the cockroach *Ectobius sylvestris* reduced its activity in the presence of cues of the nursery web spider (*Pisaura mirabilis*). Due to the high food quality (e.g. C/N-ratio), omnivorous insects may be at higher risk of predation compared with herbivores (Minagawa and Wada 1984). In addition, faster learning and longer information retention is attributed to omnivores because of a high degree of variability in food sources (Coll and Guershon 2002). The response of crickets to predator cues was largely species specific. They increased or reduced their mobility in response to chemotactile cues of different spider species. Interestingly, crickets changed their antipredator strategy towards predation risk of the nursery web spider during their life cycle: Immature crickets increased their mobility in response to *Pisaura* cues, whereas adult crickets became more immobile. Relative larger spiders that may pose a higher risk induced stronger antipredator response. More common spider species led to higher mobility in crickets compared with relatively rare species. Our results indicate that predators that are more likely to encounter prey induce stronger responses and highlight the importance of syntopic occurrence for the evolution of antipredator behaviour. Although the majority of former studies reported a reduction in prey mobility in response to predation risk (Lima 1998), our results demonstrate that a single prey species can exhibit different antipredator strategies towards different predator species. The response to a single predator species can even change during ontogeny.

The role of the experimental setting

Prey are expected to trade-off antipredator behaviour against foraging (Houston *et al.* 1993). Whereby, prey should exhibit antipredator behaviour in high-risk situations and more feeding in low-risk situations (Lima and Bednekoff 1999). Crickets under spider predation risk tended to increase food uptake and lost less weight compared to crickets in control microcosms. In addition, increased assimilation efficiency and extraction of nitrogen from food under predation risk can enhance body mass as well (Thaler *et al.* 2012). The results of our microcosm experiment suggest that prey can compensate for short-term cost of antipredator

behaviour. Chronic predation risk is likely to incur high fitness costs in the long run (e.g. on reproductive output). So far, long-term studies of fitness consequences under predation risk are still scarce (Werner and Peacor 2003). Through enhanced feeding rates of the cricket prey, predators indirectly increased herbivory within microcosms. Enhanced feeding by threatened herbivores would weaken the herbivory-reducing effect of predators on plants that is often assumed in density-mediated top-down cascades.

In the previous microcosm experiment, crickets were forced to stay on plants bearing spider cues. Under natural conditions, however, it is very likely that crickets would move to safer locations if possible. In a follow-up experiment, we offered crickets an alternative cue-free plant. Crickets indeed avoided cue-bearing plants and frequented cue-free plants more often. Consequently, herbivory was reduced on plants bearing *Pisaura* cues. Here, we detected lowest weight gain in the presence of cues of both predators (spiders and ants) and intermediate weight gain in the presence of cues from either of them. However, further experiments would be necessary to test if multiple predators induce higher fitness costs. The comparison of both lab experiments ('no-choice' microcosm *versus* plant choice experiment), demonstrates that effects of spider predation risk depend on the experimental setting. We suggest that more natural experimental settings (e.g. the offer of an alternative plant) reveal more realistic results and gain a better understanding of fitness consequences and indirect predator effects on plants.

Similar to the microcosm experiments, the behavioural arena experiments revealed contrasting results between the two experimental setups ('no-choice experiment' *versus* 'choice experiment'). For example, crickets increased their activity on filter papers bearing *Pisaura* or *Agelena* cues compared with cue-free filter papers. If crickets could choose between filter paper halves bearing *Pisaura* or *Agelena* cues and cue-free filter paper halves, we could not detect any difference in cricket behaviour. Regarding *Aulonia* cues, crickets changed their behaviour in the presence of cues in the choice experiment but not in the no-choice experiment. Similarly, we identified different species traits that were related to antipredator behaviour among the two experimental setups. We suggest that these contrasting results could be explained by the properties of chemical cues that mediate behavioural changes. For example, highly volatile cues would mitigate differences between the two filter paper halves in the choice experiment, because they diffuse in the whole arena. However, the current knowledge about the cue identity is not sufficient to explain the contrasting results across the different experimental setups. Thus, deeper insights into the chemical properties of cues that mediate such behavioural changes are desirable.

The scent of spiders and ants

Antipredator behaviour mediated by chemical cues is relatively well understood in aquatic ecosystems (reviewed in Chivers and Smith 1998; Ferrari *et al.* 2010). In terrestrial systems, the nature of spider chemical cues that mediate predator-prey interactions (kairomones and allomones) are poorly studied (Schulz 2004), except for some ant-eating specialist spiders (Cárdenas *et al.* 2012) and for the fascinating bolas spider *Mastophora cornigera* (Stowe *et al.* 1987). Our attempts to elucidate the identity of chemical compounds that induce behavioural changes in prey failed for two reasons. First, the response of crickets to *Pisaura* cues on filer papers was variable in time and fractions of the cue blend (e.g. silk only or faeces only) were not sufficient to induce behavioural changes (unpublished data; see also Eiben and Persons 2007). Second, in contrast to insects that bear mainly n-alkanes (Blomquist 2010), analysis of spider chemical cues revealed a high diversity of chemical substances (e.g. esters, unpublished data). Such compounds are very difficult to identify, especially if they are only available in small quantities (Florian Menzel, personal communication). Regarding ants, chemical cues are crucial for kin recognition and for maintaining mutualistic relationships (Howard *et al.* 1982; Lang and Menzel 2011). Ants deposit cuticular hydrocarbons while walking. These non-volatile hydrocarbons are relatively persistent (compared to alarm pheromones; Lenoir *et al.* 2009) and thus promising candidates for mediating behavioural changes. But again, the identity of chemical cues that induce behaviour in prey or other predators remain unknown and require further research (Morgan 2009; Van Mele *et al.* 2009).

If predators fear predators – towards a community approach

In classic predator-prey interaction, predators are expected to feed mainly on herbivores (Oksanen 1991). However, predators can also eat other predators (intraguild predation; Polis *et al.* 1989). Intraguild interference is particularly common in terrestrial ecosystems (Vance-Chalcraft *et al.* 2007). Spiders and ants are famous for interacting with other predators (Sanders and Platner 2007). In our ballooning experiments, juvenile spiders increased the propensity for long-distance dispersal in response to ant cues. Ballooning can be costly and spiders have only limited control of their destination (Bonte *et al.* 2012). Considering these uncertainties, the demonstrated increase in ballooning propensity highlights the impact of ants on juvenile spiders. We suggest that enhanced dispersal under ant predation risk may be the

underlying mechanism reducing spider densities in the presence of ants, which has been repeatedly demonstrated in the field (Sanders *et al.* 2011; Piñol *et al.* 2012).

In our field experiment, *Pisaura* cues induced complex changes in arthropod communities. Previous field studies on risk effects of spiders have been criticised for employing complete enclose cages (Halaj and Wise 2001). This experimental approach made natural colonisation processes impossible. The exclusion of alternative prey and enemies could have yielded unnatural cascade effects (Halaj and Wise 2001). Our new experimental approach allowed arthropods to colonise and leave experimental plants during the experimental period. Predators in particular (e.g. smaller spiders and ants), showed changes in their density on our plants. An increase in predator densities in relation to spider cues, namely the increased abundance of *Myrmica*-workers may even have reinforced risk effects of *Pisaura* cues on other arthropod groups. Our results emphasise the role of non-consumptive effects between predators in terrestrial ecosystems. They further suggest that interactions in communities are not adequately explained by trophic ladders: non-consumptive effects on one species (e.g. *Myrmica*) can modify the response of another species (e.g. *Lasius*). Communities should therefore be perceived as reticulate interaction webs rather than linear trophic chains. There is a clear need for studies that properly differentiate between density- and trait-mediated effects (*sensu* Abrams 2008) at the community level (Werner and Peacor 2003; Peacor *et al.* 2012).

The primacy of intermediate species in governing ecosystems

Trophic cascade theory predicts that predators reduce herbivory by killing herbivores (Hairston *et al.* 1960). Similarly, trait-mediated indirect effects can reduce plant damage as well (Schmitz *et al.* 1997; Trussell *et al.* 2003). We reported reduced herbivory on plants bearing spider cues from a lab and a field experiment. In the plant choice experiment, crickets did not change feeding activity in response to predation risk. Instead, they moved to cue-free plants. Consequently, herbivory was reduced on cue-bearing plants and increased on cue-free plants. We thus suggest that risk effects rather increase spatial heterogeneity than net herbivory that is expected if predators kill prey. Several recent studies demonstrated reduced herbivory under predation risk of spiders (Schmitz 1993; Chase 1996; Schmitz 1998; Rypstra and Buddle 2013). However, previous studies prevented herbivores from moving to enemy free locations or ignored the fact that they may have caused herbivory elsewhere if possible (Halaj and Wise 2001). The importance of spatial and temporal dynamics for trait-mediated

effects has already been highlighted by theoreticians (Hambäck *et al.* 2012) and empiricists (Turner and Montgomery 2003; Cronin *et al.* 2004) and should be the object of future research efforts.

As mentioned in the general introduction, ecologists have been arguing about the relative importance of top-down *versus* bottom-up control for decades. Recently, Trussell and Schmitz (2012) proposed to pay more attention to the middle of the trophic chain. Following their argument, risk effects can alter energy flow in two ways. First, predation risk can affect foraging of prey on the basal level (e.g. plants). Second, antipredator behaviour reduces food uptake by predators. While balancing between eating and being eaten, intermediated species constrain the flow of material and energy through the trophic chain (Trussell *et al.* 2006b; Schmitz *et al.* 2008). Considering our microcosm and plant-choice experiments, food uptake by threatened crickets was not affected or even increased. By contrast, predation rate of cue-experienced crickets by spiders was significantly reduced. Thus, risk effects can interrupt the transfer of energy between intermediate species and the trophic top level. They produce 'trophic heat', loss of energy from the system that would be consumed by a predator (Trussell and Schmitz 2012). The way prey perceives predation risk determines the type of cascade (density-mediated *versus* trait-mediated) and thus shapes ecosystem structure and function (Schmitz *et al.* 2004).

Acknowledgements

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Appendix

Status and author contributions of publications included in the thesis

Author affiliations

Curriculum vitae

Declaration according to §8 of the Promotionsordnung des Fachbereichs 7: Natur- und Umweltwissenschaften der Universität Koblenz-Landau, Campus Landau vom 14.06.2013

Status and author contributions of publications included in the thesis

Chapter 2
Bucher R, Binz H, Menzel F & Entling MH (in press) Effects of spider chemotactile cues on arthropod behavior. *Journal of Insect Behavior*, doi 10.1007/s10905-014-9449-1.

> MHE, FM, RB and HB conceived and designed the study. RB and HB collected the animals and conducted the experiments. RB analysed the data and wrote the manuscript. MHE, FM and HB provided statistical and editorial advice.

Chapter 3
Binz H, Bucher R, Entling MH & Menzel F (2014) Knowing the risk: crickets distinguish between spider predators of different size and commonness. *Ethology* 120:99-110.

> FM, MHE, HB and RB conceived and designed the study. HB and RB collected the animals and conducted the experiments. HB analysed the data and wrote the manuscript. FM, MHE and RB provided statistical and editorial advice.

Chapter 4
Bucher R, Binz H, Menzel F & Entling MH (in press) Spider cues stimulate feeding, weight gain and survival of crickets. *Ecological Entomology*, doi 10.1111/een.12131.

> RB, MHE, FM and HB conceived and designed the study. RB collected the study species, performed the experiments, analysed the data and wrote the manuscript. MHE and FM provided statistical and editorial advice.

Chapter 5
Bucher R, Heinrich H & Entling MH (in revision) Predator cues affect plant choice, herbivory and weight gain of wood crickets. *Entomologia Experimentalis et Applicata*.

> RB, HH and MHE conceived and designed the study. HH and RB collected the study species. HH performed the experiments. RB and HH analysed the data and wrote the manuscript. MHE provided editorial advice.

Chapter 6
Mestre L, Bucher R & Entling MH (2014) Trait-mediated effects between predators: ant chemical cues induce spider dispersal. *Journal of Zoology* 293:119-125.

> MHE, LM and RB conceived and designed the study. LM and RB collected and reared the animals. LM performed the experiments, analysed the data and wrote the manuscript. MHE and RB provided editorial advice.

Chapter 7
Bucher R, Menzel F & Entling MH (in preparation for resubmission) Risk of spider predation alters food web structure and reduces herbivory on nettles. *Oecologia*.

> RB, MHE and FM conceived and designed the experiment. RB performed the field experiment, analysed the data and wrote the manuscript. MHE and FM provided editorial advice.

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09/2009-02/2011	Graduate studies in Ecology and Evolution, with special qualification in Animal Ecology and Conservation, University of Bern, Switzerland
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08/1997-06/2004	High school, focus on Biology and Chemistry, Kantonsschule Willisau, Switzerland
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Publications

Bucher R, Heinrich H & Entling MH (in revision) Plant choice, herbivory and weight gain of crickets in the presence of predator chemical cues. *Entomologia Experimentalis et Applicata*

Uhl P, **Bucher R**, Schäfer RB & Entling MH (in preparation) Sublethal effects of Imidacloprid on interactions in a tritrophic system.

Bucher R, Menzel F & Entling MH (in preparation for resubmission) Risk of spider predation alters food web structure and reduces herbivory on nettles. *Oecologia*

Bucher R, Binz H, Menzel F & Entling MH (in press) Spider cues stimulate feeding, weight gain and survival of crickets. *Ecological Entomology*, doi 10.1111/een.12131.

Mestre L, **Bucher R** & Entling MH (2014) Trait-mediated effects between predators: ant chemical cues induce spider dispersal. *Journal of Zoology* 293:119-125.

Bucher R, Binz H, Menzel F & Entling MH (in press) Effects of spider chemotactile cues on arthropod behavior. *Journal of Insect Behavior*, doi 10.1007/s10905-014-9449-1.

Binz H, **Bucher R**, Entling MH & Menzel F (2014) Knowing the risk: crickets distinguish between spider predators of different size and commonness. *Ethology* 120:99-110.

Bucher R & Entling MH (2011) Contrasting effects of habitat fragmentation, population density, and prey availability on body condition of two orb-weaving spiders. *Ecological Entomology* 36:680-685.

Bucher R, Herrmann JD, Schüepp C, Herzog F & Entling MH (2010) Arthropod colonization of trees in fragmented landscapes depends on species traits. *Open Ecology Journal* 3:111-117.

Talks (first author is presenting author)

Bucher R, Heinrich H, Menzel F & Entling MH (upcoming) Trait-mediated indirect effects of spiders on plants. 44th Annual Meeting of the Ecological Society of Germany, Austria and Switzerland, Hildesheim, Germany

Bucher R, Heinrich H, Menzel F & Entling MH (upcoming) Trait-mediated indirect effects of spiders on plants. 28th European Congress of Arachnology, Torino, Italy

Mestre L, **Bucher R** & Entling MH (upcoming) Trait-mediated effects between predators: ant chemical cues induce spider dispersal. 28th European Congress of Arachnology, Torino, Italy

Binz H, **Bucher R**, Entling MH & Menzel F (2013) Hierarchy-dependent non-consumptive effects in ants. 2nd Global Conference on Entomology, Kuching, Malaysia

Bucher R & Entling MH (2013) Effects of habitat isolation and habitat amount on wolf spiders in agricultural landscapes. 1st Open Landscapes Conference, Hildesheim, Germany

Bucher R, Binz H, Menzel F & Entling MH (2013) Fitness consequences of antipredator behavior in crickets driven by spider cues. 19th International Congress of Arachnology, Kenting National Park, Taiwan

Bucher R, Binz H, Menzel F & Entling MH (2013) Fitness consequences of antipredator behavior in crickets driven by spider cues. 9th Ecology & Behaviour Meeting, Strasbourg, France

Mestre L, **Bucher R** & Entling MH (2013) Trait-mediated effects between predators: Ant chemical cues induce spider dispersal. 9th Ecology & Behaviour Meeting, Strasbourg, France

Bucher R, Binz H, Menzel F & Entling MH (2012) Are insects afraid of spiders? Occurrence and importance of antipredator behavior. 27th European Congress of Arachnology, Ljubljana, Slovenia

Bucher R, Binz H, Menzel F & Entling MH (2012) Are insects afraid of spiders? Occurrence and importance of antipredator behavior. 42nd Annual Meeting of the Ecological Society of Germany, Austria and Switzerland, Lüneburg, Germany

Binz H, **Bucher R**, Menzel F & Entling MH (2012) Antipredator behaviour in the wood cricket Nemobius sylvestris varies among distinct spider species and their biological traits. 105th Annual Meeting of the German Zoological Society, Konstanz, Germany

Bucher R & Entling MH (2011) Body condition of spiders in fragmented landscapes: food limitation vs. competition. 26th European Congress of Arachnology, Sede Boqer Campus, Israel

Posters (first author is presenting author)

Bucher R, Binz H, Menzel F & Entling MH (2011) Do insects smell their enemies? Searching for Non-consumptive effects. 26th European Congress of Arachnology, Sede Boqer Campus, Israel

Binz H, **Bucher R**, Menzel F & Entling MH (2011) Do insects smell their enemies? Searching for Non-consumptive effects. 41st Annual Meeting of the Ecological Society of Germany, Austria and Switzerland, Oldenburg, Germany

Krause S, Herrmann JD, Stutz S, **Bucher R**, Stocker Y, Herzog F & Schmidt-Entling MH (2010) Effects of habitat fragmentation and landscape composition on biodiversity and ecosystem services. 40th Anniversary Meeting of the Ecological Society of Germany, Austria and Switzerland, Giessen, Germany

Bucher R & Schmidt-Entling MH (2010) Effects of population density and prey availability on body condition of spiders in fragmented landscapes. 40th Anniversary Meeting of the Ecological Society of Germany, Austria and Switzerland, Giessen, Germany

Awards

Everlight Award for outstanding presentations in the field of Behaviour & Ecology, third prize, 06/2013, International Congress of Arachnology, Kenting National Park, Taiwan

Bio-logging Award for the best presentation in the foraging strategies and movement ecology session, 04/2013, Ecology & Behaviour Meeting, Strasbourg, France

Award for outstanding Matura thesis: "Effects of different agricultural management schemes on insect communities in maize fields", 06/2004, founded by the Rotary club, Kantonsschule Willisau, Switzerland

Declaration according to §8 of the Promotionsordnung des Fachbereichs 7: Natur- und Umweltwissenschaften der Universität Koblenz-Landau, Campus Landau vom 14.06.2013

Erklärung des Doktoranden darüber,

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Landau, 10. Juli 2014

Roman Bucher